Sex ratio and morphological polymorphism in an isolated, endemic Teladorsagia circumcincta population

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Sex ratio and morphological polymorphism in an isolated, endemic *Teladorsagia circumcincta* population

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Abstract

Teladorsagia circumcincta is a polygamous nematode that exhibits morphological polymorphism. Sex ratio is typically female biased and the male nematodes occur in association with the genetically similar, minor morphotypes *Teladorsagia davtiani* and *Teladorsagia trifurcata*. In experimental infections, sex ratio (proportion male) and the proportion of minor male morphs observed have been shown to be influenced by both host and nematode-related factors. As similar investigations from natural systems are rare, this study examined whether sex ratio and minor male morph frequency were associated with host age and sex and nematode infra-population size in the isolated Soay sheep population on St Kilda. Count data for *Teladorsagia* were analysed for sheep of all age classes and both sexes from the winters of three consecutive population crashes (1999, 2002 and 2005). Generally, the intensity of *Teladorsagia* nematodes increased with host age until the age of 2 years before decreasing. In 2005, abundance of nematodes was generally higher than in the previous crashes, nematode sex ratio was negatively associated with host age and tended to be negatively associated with nematode intensity. Within the male nematode subpopulation, *T. circumcincta* always predominated, followed by *T. davtiani* and then *T. trifurcata*, with little variation in the relative proportions between hosts. The presence of each minor morph was primarily associated with the intensity of male *T. circumcincta* and, in those hosts where all three male morphs were detected, intensity of each minor morph was most associated with intensity of *Teladorsagia* females. Therefore, in a year when the nematode was generally more abundant, sex ratio appeared to be influenced by both host and nematode-related factors, whereas in all years examined, the frequency of morphological polymorphism was primarily density dependent.

Introduction

In populations of dioecious parasitic nematodes, reproductive success depends on the type of mating system, the abundance and distribution of males and females in the host and their sex ratio (Haukisalmi *et al.*, 1996). Female mating probability is higher in polygamous than monogamous systems (May & Woolhouse, 1993), and in polygamous systems, female biased sex ratios occur more commonly than male-biased ratios (Poulin, 2007). *Teladorsagia circumcincta* is an example of a polygamous nematode with female-biased population structure and is often used in experimental studies (Stear *et al.*, 1997). Waller & Thomas (1978) found that, in this nematode, temporal change in sex ratio is

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mainly due to the fact that females survive longer than males inside the host. However, there is some evidence from other species that sex ratio is also density dependent. Poulin (1997) conducted a meta-analysis of data from experimental infections using polygamous nematodes, which showed that high-intensity burdens were more male biased, although a comparative analysis from natural infections provided no support for this result.

Male nematode mating strategy is also potentially important to reproductive success. Males locate females of the same species by chemotaxis (Huettel, 2004) and have been observed to engage in characteristic behaviour using the copulatory structures of the tail region to orientate and secure the female (Lee & Atkinson, 1976). In some trichostrongylid nematodes, these copulatory structures show morphological polymorphism where the males of one species have two or more morphotypes (Lancaster *et al.*, 1983; Lichtenfels & Hoberg, 1993). In *T. circumcincta*, two genetically similar minor male morphotypes, *Teladorsagia davtiani* and *Teladorsagia trifurcata*, co-occur with the classic form (Andrews & Beveridge, 1990; Stevenson *et al.*, 1996; Leignel *et al.*, 2002; Grillo *et al.*, 2008), but whether the male morphotypes adopt alternative mating strategies, as observed in some other trimorphic invertebrates (Rowland & Emlen, 2009), is not known. Observations from experimental infections have shown that the minor morphs are generally less efficient at infecting the host than the *T. circumcincta* morph (Cabaret, 1984; Richard & Cabaret, 1993; Suarez *et al.*, 1995), and the infective minor morph larvae show lower survivorship at cold temperatures (Suarez *et al.*, 1995). Also, Suarez *et al.* (1995) and Leignel & Cabaret (2001a) found that a higher proportion of the minor morphs was found in more susceptible sheep with high-intensity infections.

Experimental *T. circumcincta* infections have therefore shown that sex ratio and the proportion of minor male morphs observed are influenced by both host and nematode-related factors. However, artificially high infections may not simulate the rate of establishment (Gaba *et al.*, 2006) or adult sex ratio (Poulin, 1997) in nematodes observed in natural infections. Also, extrinsic factors have been shown to influence morphotype ratio. The prolonged cold storage of infective larvae in the laboratory is known to affect survival of the minor male morphs (Suarez *et al.*, 1995), and infections from livestock systems have shown that anthelmintic control has an indirect effect on the proportions of the minor morphs in the adult population (Leignel & Cabaret, 2001a, b). As there are no comprehensive studies on the dynamics of sex ratio and morphological polymorphism in *T. circumcincta* in the wild, this study analysed both phenomena in the Soay sheep population on St Kilda, an undisturbed host–parasite system with ten endemic species of gastrointestinal nematode (Wilson *et al.*, 2004; Craig *et al.*, 2006). The study aimed to explore to what extent *Teladorsagia* sex ratio (proportion male) and the presence and intensity of each minor male morphotype are explained by the variables year of sampling, host age and sex and intensity of con-specific nematodes.

Materials and methods

Study area and host population

The focus of the study is the Village Bay area of Hirta (638 ha), the largest island of the St Kilda archipelago (57°49′N, 08°34′W) off the coast of Scotland. This remote site is the stronghold of the Soay sheep population that has survived unmanaged for hundreds of years and which has been studied continuously since 1985 (Clutton-Brock & Pemberton, 2004). The population is subject to extreme fluctuations with population crashes occurring when sheep numbers exceed food supply. This study used post-mortem worm count data from sheep that died in the crashes of 1999, 2002 and 2005 when the population decreased by 53, 52 and 32%, respectively, from the previous to the following August, based on island counts. At the time of sampling in the winter/spring months, lambs, yearlings, 2-year olds and adults were around 10, 22, 34 and >34 months old, respectively (table 1).

Collection and identification of nematodes

Nematodes were recovered from dead sheep and quantified as outlined by Craig *et al.* (2006). Two species of nematode occur in the abomasum, *Teladorsagia* and *Trichostrongylus axei*. Female *Teladorsagia* were differentiated from female *T. axei* by size and the presence of papillae on the neck region (*T. axei* females have a notch), and *Teladorsagia* males were differentiated from *T. axei* and into morphotypes *T. circumcincta* (synonym *Ostertagia circumcincta*), *T. davtiani* and *T. trifurcata* (synonym *Ostertagia trifurcata*) based on spicule and tail morphology. *Teladorsagia circumcincta* spicules are long and slender (fig. 1a). The minor morphs *T. trifurcata* and *T. davtiani* share similar short, stout spicules that have a thick median spine (fig. 1b). Further differentiation between the minor morphs was based on features of the dorsal part of the genital cone in accordance with Rose (1962) and Becklund & Walker (1971); *T. trifurcata* has a prominent accessory bursal membrane supported by two rays (fig. 1c), whereas *T. davtiani* lacks an obvious membrane but exhibits two terminal protuberances on the cone (fig. 1d). Grillo *et al.* (2008) have previously provided population genetic evidence that the three *Teladorsagia* male types in this population are morphological variants of the same species.

Table 1. Sample sizes of Soay sheep from which *Teladorsagia* counts were obtained.

Host age	Host sex	1999	2002	2005	Total
Lambs	Male	12	12	5	29
	Female	12	12	6	30
Yearlings	Male	5	7	4	16
	Female	6	6	5	17
2-year-olds	Male	6	11	6	23
	Female	2	8	3	13
Adults	Male	6	6	4	16
	Female	6	7	6	19
Total		55	69	39	163

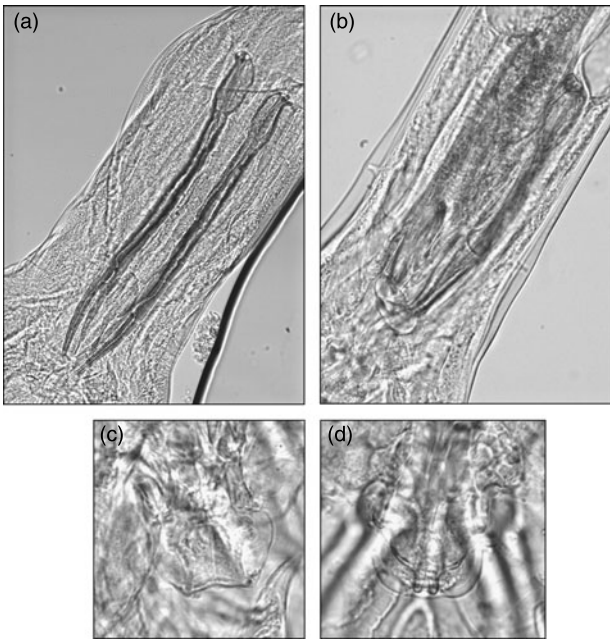

Fig. 1. Morphological variation in *Teladorsagia*. (a) Adult male spicules of *Teladorsagia circumcincta*; (b) adult male spicules of *Teladorsagia trifurcata* and *Teladorsagia davtiani*. Posterior end of minor male morphs; (c) *T. trifurcata*, showing accessory bursal membrane supported by two rays; (d) *T. davtiani*, showing tuberosity on genital cone.

Statistical analyses

All statistical analyses were conducted on S-Plus version 6.2.1 (Insightful Corp., Seattle, Washington, USA) and GenStat Release 11.1 (VSN international Ltd, Hemel Hempstead, UK). For each model, the error structure (normality and constant variance) was evaluated graphically using the appropriate diagnostic plots (Crawley, 2003).

Total intensity of Teladorsagia

In order to test whether there was a significant difference in total *Teladorsagia* burden between crash years, a generalized linear model (GLM) with log link function and negative binomial error structure was fitted with count as the response variable and age, age^2 (fitted as a quadratic to account for the fact that intensity increases until the age of 2 years before decreasing, see Craig *et al.*, 2006), host sex and crash year (as a factor) as explanatory variables.

Sex ratio (proportion male) of Teladorsagia

Sex ratio of *Teladorsagia* in each host was calculated as the proportion of males (males/(males + females)). Analysis of sex ratio was performed according to the method of Wilson & Hardy (2002). A GLM (weighted regression using individual totals of male plus female nematodes as weights) with binomial error structure and logit link function was fitted with age, host sex, year (as a factor) and intensity of infection and all possible interactions as the response variables. The model was simplified by step-wise removal of non-significant terms using *F*-tests to account for overdispersion, as described by Wilson & Hardy (2002).

Relative proportions of each male Teladorsagia *morphotype*

For illustration, the relative proportions of each male morphotype were calculated for each age class of sheep and for all sheep across all years by dividing the sum of each morph found by the sum of all male *Teladorsagia*, regardless of morphotype, within the particular age class, multiplied by 100 to give a percentage. Standard error for each proportion was calculated according to Fowler & Cohen (1990).

Prevalence and intensity of each minor male Teladorsagia *morphotype*

Prevalences of *T. davtiani* and *T. trifurcata* were analysed using a GLM with logit link function and binomial error structure with the presence or absence of each morph as a binary response (zero vs. non-zero counts), and tested for associations with host age, host age^2, host sex, year (as a factor) plus intensities of the *T. circumcincta* male morph and *Teladorsagia* females as explanatory variables (excluding interactions).

Count data for *T. davtiani* and *T. trifurcata* were highly aggregated and best modelled using a linear model on log-transformed count data (excluding the zero counts) as the response variable and host age, host age^2, host sex, year (as a factor) plus intensities of *T. circumcincta* male morph and *Teladorsagia* females as explanatory variables (excluding the interactions).

Results

Total intensity of Teladorsagia

Teladorsagia intensity increased with age until the age of 2 years and then decreased ($\chi^2_1 = 22.36$, $P < 0.0001$). There was also an association with year; intensity was higher in 2005 than in the two previous crash years of 2002 and 1999 ($\chi^2_2 = 8.18$, $P = 0.017$; the final model explained 25.46% of the deviance; fig. 2). There was no significant association with host sex.

Sex ratio (proportion male) of Teladorsagia

There was a significant interaction between host age and year on sex ratio (proportion male) ($F_{2,160} = 8.63$, $P = 0.0003$; final model explained 15.63% of the variance). Due to the effect of year, sex ratio was also analysed within year and, in 2005, a negative association with host age ($F_{1,37} = 10.35$, $P = 0.002$) and a marginally significant negative association with *Teladorsagia* intensity ($F_{1,37}$, $P = 0.056$; final model explained 32.77% of the variance) were found. In 1999 and 2002, no such associations were found and sex ratio was not associated with host sex in any year (table 2 and figs 2 and 3).

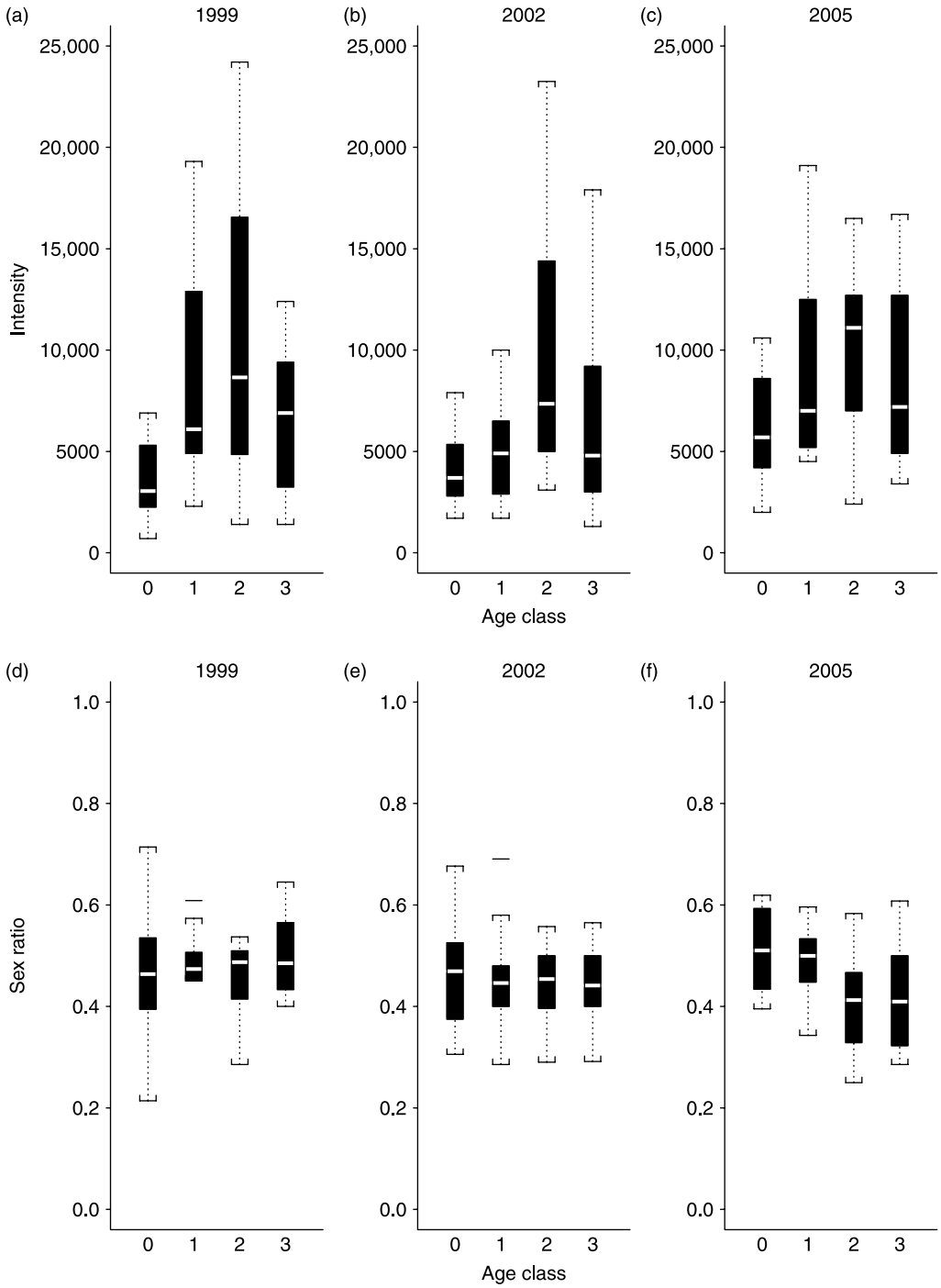

Fig. 2. *Teladorsagia* intensity (a–c) and sex ratio (d–f; proportion male) by age class for each year (0, lambs; 1, yearlings; 2, 2-year-olds; 3, older than 2 years).

The relative proportions of each male Teladorsagia *morphotype*

The proportions of each *Teladorsagia* male morph were calculated for each age class and across all hosts. Across all hosts in the study, the morphs always occurred in similar relative proportions; *T. circumcincta* made up 81.4% of all males, followed by *T. davtiani* at 14.39% and *T. trifurcata* at 4.21% (table 3 and fig. 4).

Table 2. Summary of significant results from generalized linear model, with binomial error structure, testing for association between sex ratio (proportion male) and host age, sex and year and all possible interactions (*F* statistics were used to account for overdispersion).

Year	Response variable	Explanatory variable	*F*-value	df	Pr (*F*)	Association
All years	Sex ratio	Age	5.11	1	0.025	Proportion of males decreased with age in 2005
		Year	3.54	2	0.031	
		Age: year	8.63	2	0.0003	
2005	Sex ratio	Age	10.35	1	0.002	Proportion of males decreased with age
		Teladorsagia intensity	3.89	1	0.056	Proportion of males decreased with intensity

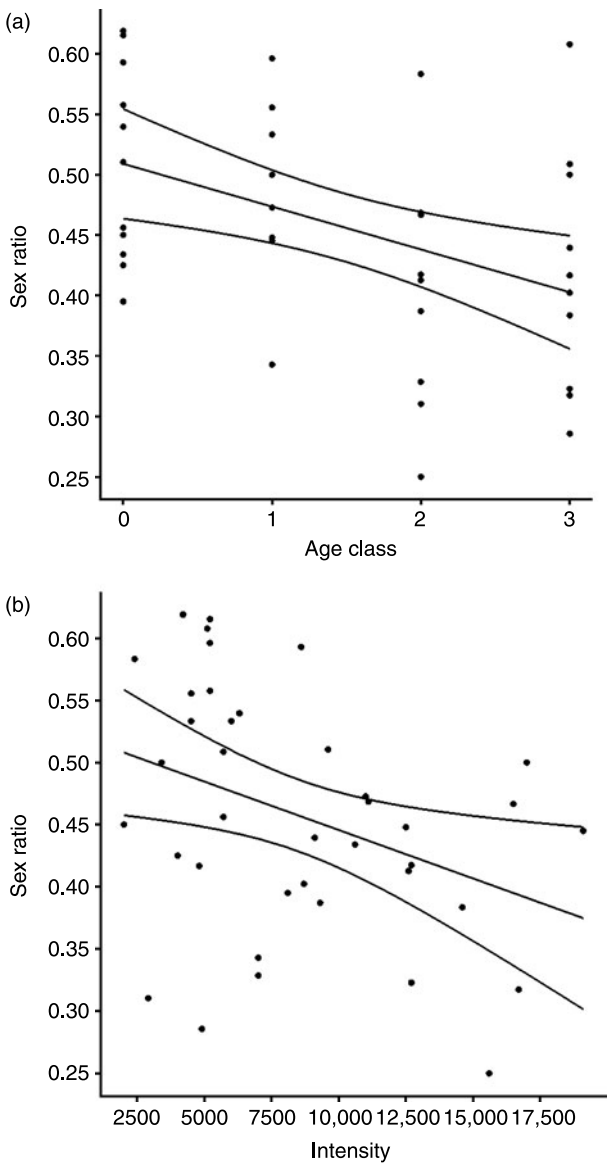

Fig. 3. Association between *Teladorsagia* sex ratio (proportion male) and (a) host age and (b) nematode intensity within all sheep sampled in 2005 ($n = 39$; line fitted with 95% confidence limits).

Prevalence and intensity of each minor male Teladorsagia *morphotype*

Across all hosts ($n = 163$), prevalence of the *T. circumcincta* male morph was 100%, *T. davtiani* was 91.41% and *T. trifurcata* was 61.35%. Presence of *T. davtiani* was associated with intensity of *T. circumcincta* males ($\chi^2_1 = 17.79$, $P < 0.0001$; final model explained 23% of the deviance) and *Teladorsagia* females ($\chi^2_1 = 4.24$, $P = 0.04$; final model explained 23% of the deviance). Similarly, the presence of *T. trifurcata* was associated with intensity of *T. circumcincta* males ($\chi^2_1 = 10.30$, $P = 0.001$; final model explained 4.7% of the deviance). None of the other explanatory variables, namely host sex, age (also fitted as a quadratic) or year, was associated with the presence of either minor male morph (table 4).

Intensity of *T. davtiani* was explained by intensity of *T. circumcincta* males ($F_{1,146} = 13.26$, $P < 0.0005$) and by intensity of *Teladorsagia* females ($F_{1,146} = 109.33$, $P < 0.0001$; final model explained 45.64% of the variance). Intensity of *T. trifurcata* was explained by intensity of *Teladorsagia* females ($F_{1,97} = 6.93$, $P = 0.009$; final model explained 11.08% of the variance). Neither host sex, age (also fitted as a quadratic) nor year was associated with intensity of *T. davtiani* or *T. trifurcata* (table 4).

Discussion

The notoriety of *T. circumcincta* as a pathogenic parasite of sheep (Stear *et al.*, 2007) has prompted much research into the species at the population level (Stear *et al.*, 1997). Sex ratio and frequency of male morphological polymorphism are dynamic aspects of the population structure and potentially important to the fitness of the parasite. Experimental infections have shown that both host and nematode-related factors can influence these characteristics; however, there have been no comprehensive studies from the wild. To address this, both sex ratio and morphological polymorphism in an endemic population of *T. circumcincta* infecting the wild Soay sheep of St Kilda were analysed for association with host age and sex and nematode infra-population size.

In a previous study using post-mortem nematode count data from the host population crashes of 1999 and 2002, *T. circumcincta* intensity was found to increase in hosts until the age of 2 years before decreasing, with no difference between the sexes or between years (Craig *et al.*, 2006). The addition of data from 2005 has confirmed this pattern in the host, but shown that the parasite was generally more abundant in 2005 than it was in 1999 and 2002 (fig. 2). In 2005 only, sex ratio (proportion male) was

Table 3. Mean intensity (±SE) of *Teladorsagia* nematodes recovered from sheep of both sexes and different age classes across all years (see table 1). Male nematodes are separated according to morphotype with relative proportions given in parentheses.

	Teladorsagia mean count ± SE				
		Male (proportion % of morphotype ± SE)			
	Female	*Teladorsagia circumcincta*	*Teladorsagia davtiani*	*Teladorsagia trifurcata*	Total
Lambs	2302 ± 155	1647 ± 116 (79.22 ± 0.11)	308 ± 35 (14.83 ± 0.10)	124 ± 25 (5.95 ± 0.07)	4381 ± 282
Yearlings	3884 ± 461	2803 ± 305 (80.10 ± 0.12)	590 ± 94 (16.87 ± 0.11)	106 ± 20 (3.03 ± 0.05)	7384 ± 843
2-year-olds	5594 ± 558	3738 ± 405 (83.16 ± 0.09)	553 ± 76 (12.30 ± 0.08)	204 ± 36 (4.54 ± 0.16)	10089 ± 1011
Adults	3977 ± 463	2629 ± 258 (82.59 ± 0.11)	457 ± 68 (14.36 ± 0.10)	97 ± 21 (3.05 ± 0.05)	7160 ± 744
All sheep	3709 ± 213	2554 ± 142 (81.40 ± 0.05)	451 ± 33 (14.39 ± 0.05)	132 ± 14 (4.21 ± 0.03)	6848 ± 375

negatively associated with host age and tended to be negatively associated with nematode intensity (table 2 and figs 2 and 3). The fact that this was not found in 1999 or 2002, when general abundance was lower, may either suggest that this result is a statistical artefact or that a threshold level of intensity is required to detect an association. If real, the decrease in male nematode proportion with host age could be explained by differential mortality between the sexes. Waller & Thomas (1978) found a reduction in the proportion of *T. circumcincta* male nematodes over time in domestic lambs and considered this to be due to greater susceptibility of male worms to the effects of the host immune system. The weak negative association of sex ratio (proportion male) and nematode intensity found in this study contradicts the findings of Poulin (1997), whose meta-analysis of data from experimental infections gave the opposite result. However, the comparative analyses in natural infections did show a similar trend to the findings reported in this study (Poulin, 1997). To our knowledge, this is the first time that host age as well as nematode intensity have been associated with sex ratio in a natural *T. circumcincta* infection.

Within the male nematode population, three morphotypes exist; the predominant *T. circumcincta* morph and the minor morphs *T. davtiani* and *T. trifurcata*. This study examined the frequency of the minor male morphs and their association with the host and nematode infrapopulation, which is more detailed than most surveys that tend not to differentiate between the minor morphs (Becklund, 1962; Lichtenfels & Hoberg, 1993; Drozdz, 1995). Considering the fact that intensity of *Teladorsagia* varies with host age, it is interesting to note that the three morphotypes always occurred in more or less fixed proportions. This was first shown in a previous study using data from the 1999 and 2002 population crashes (Craig *et al.*, 2006). With the addition of data from 2005, this study showed that, within the male population, *T. circumcincta* predominated constituting 81.4%, *T. davtiani* was the second most frequent morph with 14.36%, followed by the comparatively rarer *T. trifurcata*, which only constituted 4.21% in all hosts examined (table 3 and fig. 4).

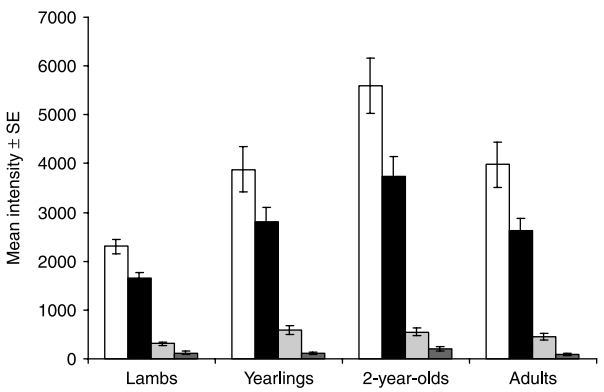

Fig. 4. Mean intensity (±SE) of *Teladorsagia* nematodes by sex and male morphotype recovered from sheep of both sexes and different age classes across all years (see tables 1 and 3). □, *Teladorsagia* female; ■, *Teladorsagia circumcincta* male; ▒, *Teladorsagia davtiani* male; ▓, *Teladorsagia trifurcata* male.

Neither host age nor sex affected the prevalence or intensity of the minor morphs. The presence of the minor morphs was mainly associated with intensity of the male *T. circumcincta* morph and, in hosts where all morphs occurred, intensity of the minor morphs was more associated with intensity of females (table 4). In experimental infections, Suarez *et al.* (1995) and Leignel & Cabaret (2001a) found that a higher proportion of the minor morphs were found in more susceptible sheep, and that intensity of infection was the most important factor in explaining frequency of occurrence of the minor morphs.

It is not known whether the male morphotypes of *T. circumcincta* adopt alternative mating strategies in the host. Artificial selection of the minor morphs (not differentiated) has been achieved by mating them with virgin females, from the previously selected progeny, resulting in an orderly increase in incidence of the minor morph and an orderly decrease in incidence when selection ceased (Lancaster *et al.*, 1983). If the morphs adopt alternative mating strategies, it could partly explain why they occur in characteristic proportions. If the morphological traits (fig. 1) are inherited and there is an underlying cost to being a minor morph, it is possible that natural selection shapes the relative proportions of the morphs observed in the field. Although it was not possible to examine the effects of season on the frequency of morphological polymorphism in *T. circumcincta* in the Soay sheep population, evidence from field surveys in France indicated a seasonal influence, where a higher proportion of the minor morphs were recorded in autumn than in spring, suggesting lower overwinter survivorship (Cabaret *et al.*, 1984; Suarez *et al.*, 1995).

Table 4. (A) Results of a generalized linear model (GLM), with binomial error structure, testing for an association between host age (also as quadratic), sex, year, intensity of *Teladorsagia circumcincta* males, *Teladorsagia* females and presence/absence of either *Teladorsagia davtiani* or *Teladorsagia trifurcata* males. (B) Results of linear model (LM), with normal error structure, testing for an association between the same explanatory variables as above and intensity (log transformed counts >0) of each minor morph.

(A) Results of a GLM

Morph as response (presence/absence)	Explanatory term	ΔDeviance	df	Pr (Chi)	Association
T. davtiani male	*T. circumcincta* male	**17.79**	**1**	**< 0.0001**	Minor morph more likely to occur in high-intensity infections
	Teladorsagia female	**4.24**	**1**	**0.039**	
	Age	2.85	1	0.09	–
	Age^2	0.06	1	0.80	–
	Sex	0.54	1	0.46	–
	Year	2.87	2	0.24	–
T. trifurcata male	*T. circumcincta* male	**10.30**	**1**	**0.001**	Minor morph more likely to occur in high-intensity infections
	Teladorsagia female	1.48	1	0.22	–
	Age	1.00	1	0.31	–
	Age^2	2.00	1	0.16	–
	Sex	2.07	1	0.15	–
	Year	5.02	2	0.08	–

(B) Results of a LM

Morph as response (intensity)	Explanatory term	*F* value	df	Pr (*F*)	Association
T. davtiani male	*T. circumcincta* male	**13.26**	**1**	**0.0004**	Intensity of minor morph positively associated with intensity of major morph and of females
	Teladorsagia female	**109.33**	**1**	**< 0.0001**	
	Age	1.52	1	0.21	–
	Age^2	0.06	1	0.80	–
	Sex	0.01	1	0.90	–
	Year	0.77	2	0.46	–
T. trifurcata male	*T. circumcincta* male	0.86	1	0.35	–
	Teladorsagia female	**6.93**	**1**	**0.009**	Intensity of minor morph positively associated with intensity of major morph
	Age	0.01	1	0.90	–
	Age^2	0.79	1	0.37	–
	Sex	4.00	1	0.06	
	Year	1.01	2	0.37	–

Significant results are highlighted in bold. Dashes denote non-significance.

Taken together, these results show that, in a year of generally higher *Teladorsagia* abundance, nematode sex ratio (proportion male) was associated with host age and nematode intensity. The *Teladorsagia* population became more female biased with increasing host age and to some extent increasing nematode intensity. If this was due to higher mortality of males than females, all male morphotypes were apparently equally susceptible, as the relative proportions were not affected by host age. The frequency of occurrence of the minor morphs was most associated with intensity of nematodes. Further research is required to ascertain whether the different morphotypes have alternative mating strategies and whether their mating probability is influenced by sex ratio.

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